

SMALL FOSSIL VERTEBRATES FROM VICTORIA CAVE, NARACOORTE, SOUTH AUSTRALIA IV. REPTILES

by MEREDITH J. SMITH

Summary

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Reptile fossils have been found at Naracoorte, South Australia, in a Pleistocene cave deposit that is rich in marsupial and rodent remains. Reptile vertebrae are abundant and a few jaws and limb bones have been recovered. The diagnostic features of these bones are described.

Of the twelve reptile species present, nine still live in the Naracoorte area; they are three elapid snakes, *Pseudonaja* c.f. *P. nuchalis*, *Notechis* c.f. *N. scutatus*, and *Pseudechis* c.f. *P. porphyriacus*; and six lizards, *Varanus varius*, *V. gouldii*, *Trachydosaurus rugosus*, *Tiliqua nigrolutea*, *Egernia* c.f. *E. whitei* and a species consistent with *Sphenomorphus tympanum*. A fourth elapid snake represented by 40 isolated vertebrae, and a species of *Amphibolurus* have not been identified.

The remaining species is a boid snake, described here as a new genus and species, *Wonambi naracoortensis*. The eight vertebrae recovered are large, suggesting a length of at least 5 m for the whole snake. Morphologically, the vertebrae differ strongly from those of other Australian booids in having a high but back-sloping neural spine, paracotylar foramina present, accessory processes absent, and, particularly, in having large paradiapophyses that extend further laterally than the zygapophyses. These vertebrae closely resemble those of *Madstoa bai* Simpson from the Eocene of Patagonia, but without cranial remains of both species, no relationship can be postulated between *Wonambi* and *Madstoa*.

Introduction

The reptile faunas of Australian fossil deposits have rarely been completely analysed. For some deposits, the presence of unidentified reptiles has been noted (e.g. Archer 1974, Dorch & Merrilees 1971, Gill & Banks 1956, Lundelius 1963); for other deposits, the most distinctive species have been identified, but often to genus only (e.g. Merrilees 1968; Thorne 1971). Exceptions are the carpet snake, *Python variegatus* (= *Python spilotus variegatus*) associated with the extinct marsupial, *Thylacoleo* sp., and other marsupial remains at Marmor Quarry, Queensland (Longman 1925) and the sleepy lizard, *Trachydosaurus rugosus*, at Gore Limestone Quarries, Queensland (Longman 1945). Remains of a large extinct varanid lizard, *Megalania prisca*, have been found in Pleistocene deposits in Queensland, New South Wales and central Australia (Fejervary 1918, 1935; Hecht 1975).

The deposit in Victoria Cave at Naracoorte, South Australia, is probably of Pleistocene age (Smith 1971). Among the large animals, extinct species are common (van Tets & Smith 1974; Wells, pers. comm.), but, in contrast, the small marsupials and small birds are referable to modern species, though not all of them occur in the Naracoorte area now (Smith 1971, 1972; van Tets & Smith 1974).

For identifying reptile species, characteristics of skull fragments, jaws and teeth are of less value than they are for mammals. As reptiles grow throughout life and are polyphyodont, the "adult" dentition cannot be defined as it can in mammals. The variations in dentition between species in many genera is no greater than within species. Fortunately the vertebrae of reptiles are of diagnostic value and Auffenberg (1963) was able to identify single vertebrae of North American snakes to genus and often to species. Diagnostic vertebral characters have

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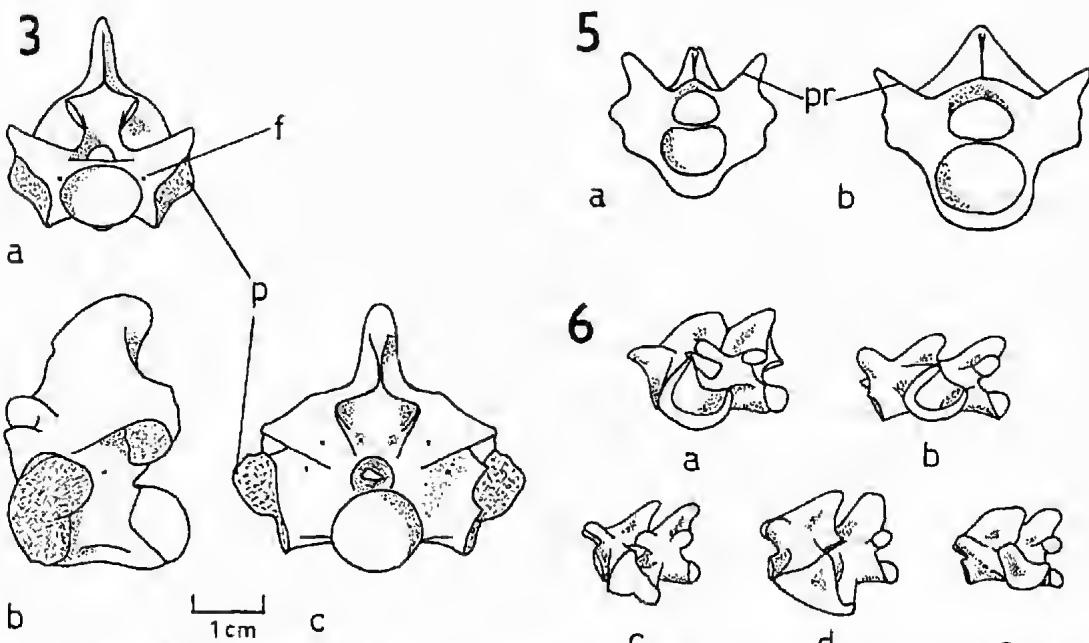
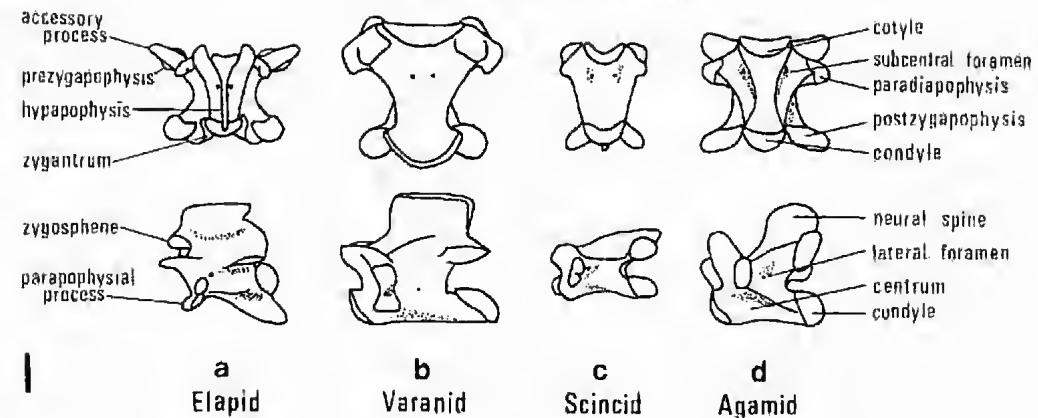


Fig. 1. Ventral (above) and lateral views of precaudal vertebrae of (a) *Pseudonaja nuchalis* (Elapidae), (b) *Varanus gouldii* (Varanidae), (c) *Tiliqua occipitalis* (Scincidae), (d) *Amphibolurus barbatus* (Agamidae).

Fig. 3. Vertebrae of *Wonambi naracoortensis* are distinguished by their wide paradiapophyses (p) and presence of paracotylar foramina (f) as seen in (a) anterior view of P16144k and (b) lateral, and (c) posterior view of P16144k.

Fig. 5. The prezygapophysial facets are less upturned in *Trachydosaurus rugosus* (b) than in *Tiliqua nigrolutea* (a).

Fig. 6. Distally, the fused sacral pleurapophyses are cup-shaped in *Trachydosaurus rugosus* (a) and *T. occipitalis* (b) but are triangular in *T. nigrolutea* (c), *T. scincoides* (d) and *Egernia cunninghami* (e).

not been established precisely for any Australian snake species (Smith 1975). Fossil remains of lizards include not only skull bones and vertebrae but also some limb bones and some elements of pectoral and pelvic girdles. These are briefly described, and their diagnostic values assessed in this paper.

Methods

Methods of collection and preservation follow Smith (1971).

The present maximum depth of excavation is 80 cm, although bone chips occur in cores taken as deep as 2.5 m.

TABLE 1

Some dimensions of the holotype (P16168) and the seven paratype vertebrae of *Wonambi naracoortensis*
(Dimensions in mm)

	Specimen							
	P16168	P16170a	P16166	P16129t	P16144k	P16144s	P16167	P16170b
Length between zygapophyses	16.5	15.4	18.1	16.4	19.3	21.8	23.4	19.6
Height (centrum + neural spine)	32.3	34.1*	40.8*	33.1	38.4	37.1	41.0	36.2
Width across prezygapophyses	25.6	21.1	27.7	25.8	30.4	33.0	35.5	29.5
Width across paradiapophyses	28.5	22.3	29.7	27.7	33.2	41.1	43.7	33.0
Minimum width of centrum	18.6	15.9	21.2	19.1	22.7	24.1	27.1	21.8
Width of zygosphene	9.2	8.4	11.8	9.3	12.6	10.9	12.4	11.3
Width of condyle	10.8	8.2	10.6	10.3	12.6	12.3	12.7	12.4
Length of prezygapophysis	8.1	6.1	7.5	7.4	8.9	11.8	12.8	10.9

* Height includes length of hypapophysis.

Skull and jaw elements of all but the most robust species were rarely recovered from the Victoria Cave deposit, whereas vertebrae were common. Consequently, for the diagnosis of reptile species in this fauna, vertebrae have been considered in detail and other bones more briefly. Comparisons have been made with dry, disarticulated skeletons, and occasionally with cleared, alizarin-stained whole specimens.

Descriptive terms (Fig. 1) follow Auffenberg (1963). The "length" referred to in descriptions of vertebrae is the greatest distance from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis (Pr-Po of Smith 1975). The ranges of lengths are given, with mean and standard error. Measurements were made to the nearest 0.1 mm, with dial-reading, needle-point calipers. The fossil specimens are lodged in the South Australian Museum (SAM).

Results

Family BOIDAE

Boid vertebrae lack parapophysial processes, the accessory processes are very short or absent and the vertebrae lack hypapophyses on the posterior two thirds of the precloacal column (Hoffstetter & Gase 1969).

Wonambi n. gen.

Definition: Vertebrae characterized by a high, backwardly-sloping neural spine; slightly upturned zygapophysial facets; large paradiapophyses extending laterally beyond the zygapophyses; and a pair of paracotylar foramina.

Type species: *Wonambi naracoortensis*

Content: *W. naracoortensis* is the only known species in the genus.

"*Wonambi*" is derived from an aboriginal name for the mythical rainbow serpent (Elkin 1964).

Wonambi naracoortensis n. sp.

Holotype: SAM, P16168. A dorsal vertebra collected in Fossil Chamber, Victoria Cave, Naracoorte, S. Aust., at a depth not greater than 30 cm below the surface of the cave earth.

Definition: The same as for the genus *Wonambi* until other species are described.

Description: The neural spine is high (Fig. 2C); its anterior edge begins near the rim of the zygosphene and rises obliquely to the horizontal dorsal edge of the spine. The spine overhangs slightly posteriorly. The zygosphene is narrow (Table 1) but it is so heavily thickened that it is as deep in dorsoventral extent as it is broad. The zygosphenal facets are almost vertical (c. 70° to horizontal) (Fig. 2D). The relatively small zygapophyses are slightly upturned (c. 25° from horizontal). Accessory processes are completely absent. The paradiapophyses are large (Table 1); the upper part of the articular facet is convex and protrudes so far from the centrum that the maximum width of the vertebra is the width measured across the paradiapophyses; the lower part of the articular facet is flat. The cotyle and condyle are slightly depressed (Fig. 2A) and the top of the condyle is tilted forwards at c. 75° to the vertical. The ventral surface of the centrum is smoothly rounded, with weak subcentral ridges and a low median ridge that terminates posteriorly as a blunt haemal keel, notched in the midline (Fig. 2B).

Each foramen of the subcentral pair is located close to the median ridge at about mid-centrum; each foramen of the lateral pair lies on the neural arch pillar about halfway between paradiapophysis and postzygapophysis. There appear to be two pairs of parazygantral foramina, but, as the bone is pitted in this region,

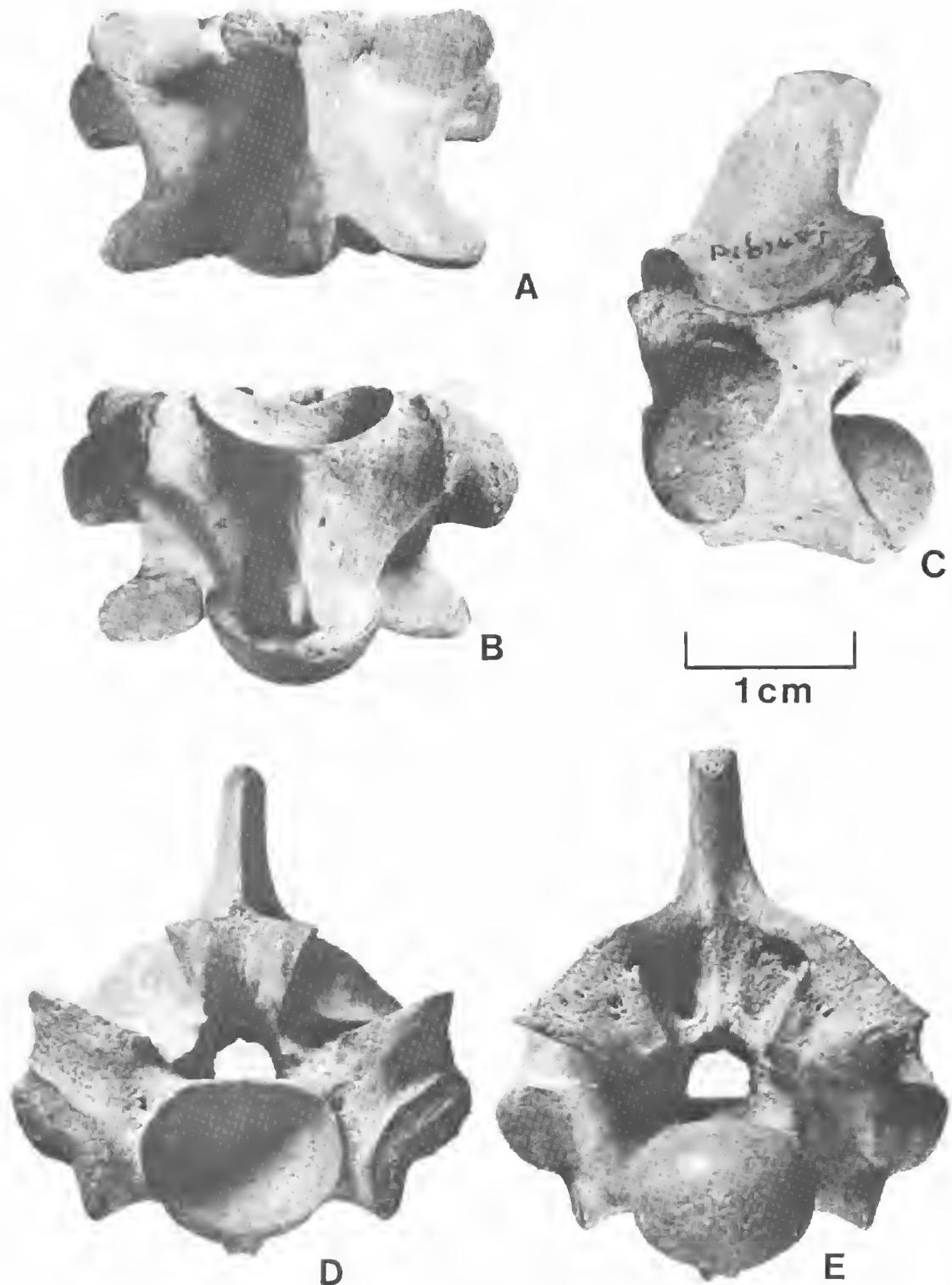


Fig. 2. The holotype of *Wonambi naracoortensis* (P16168) in dorsal (A), ventral (B), lateral (C), anterior (D), and posterior (E) views.

foramina are distinguished with difficulty from pits. The two foramina of a paracotylar pair lie close to the rim of the cotyle near the top of the centrum.

Variation: The paratype series consists of seven dorsal vertebrae, P16129t, P16144k,s, P16166-7, and P16070a, b all but one of which were found in the top 30 cm of the cave earth of Fossil Chamber, Victoria Cave. All specimens share with the holotype the diagnostic features, especially the widely spaced paradiapophyses (Table 1, Fig. 3). The parzygantral foramina consist of a single pair which are sunk into hollows in P16129s, P16167 and P16170b; and in P16144k the single pair of zygantral foramina can be seen clearly. The haemal keel is notched posteriorly in P16129s, P16167 and P16170b (as in the holotype), these vertebrae having occurred nearer the tail than the others, as judged from their lower neural spines. P16166 bears a small hypapophysis, and P16170a a longer hypapophysis.

Associated material: A fragment (P16170c) from near the anterior end of a left maxilla with three teeth, curved backwards. Each tooth is approximately 7 mm long.

Assuming that P16167 represented the largest vertebra of the specimen of *Wonambi naracoortensis*, and assuming that the largest vertebrae of *W. naracoortensis* and *Python spilotus*, respectively, occupy the same proportion of the length of the vertebral column, then P16167 would have been derived from a snake of total length about 5.0 m.

Comparison with other species: Of the eight Australian species of Boidae, vertebrae of *Python spilotus* (4 specimens), *P. amethistinus* (2), *Liasis childreni* (1), *Chondropython viridis* (1) and *Aspidites melanocephalus* (3) have been examined.

The vertebrae of these extant boids are characterized by the presence of small, pointed, accessory processes beneath the prezygapophyses, by having large outwardly-directed zygapophyses extending further laterally than the paradiapophyses (Table 2) and the neural spine hatchet-shaped, and by the absence of paracotylar foramina. Subcentral ridges are strongly developed. The general shape of the vertebra is similar among all the species (Tables 2, 3). *Chondropython viridis* differs in having the neural spine bifurcate anteriorly.

Python spilotus and *P. amethistinus* resemble each other in having a pair of foramina at the base of the neural spine, while *Aspidites*

melanocephalus, *Chondropython viridis* and *Liasis childreni* lack this pair of foramina.

Wonambi naracoortensis differs from all other Australian boids in lacking accessory processes, in having the neural spine sloping backwards, in having weak subcentral ridges, and in the presence of paracotylar foramina. It shares with *Aspidites melanocephalus*, *Chondropython viridis* and *Liasis childreni* the absence of foramina at the base of the neural spine. The total height (relative to length) of the vertebrae is greater in *W. naracoortensis* than in other Australian boids, the paradiapophyses extend further laterally than the zygapophyses, the condyle (relative to vertebra length) is wider and the zygosphene (relative to vertebra length) is narrower (Table 2). On the other hand, width across prezygapophyses, minimum width of centrum, and length of prezygapophysis (all relative to vertebra length) fall within the ranges of the extant species, as does height/width of condyle (Table 3).

Paracotylar foramina are generally absent in extant boids, and occur only in the genera *Constrictor* and *Tropidophis* (Boinae) and *Enygrus* (Erycinae) (Hoffstetter & Gayrard 1964). They are found, usually as two pairs, in the fossil genera *Gigantophis* and *Madstoa* (Hoffstetter 1961a, b), and as a single pair in *W. naracoortensis*.

Whereas the lengths of vertebrae of *Wonambi naracoortensis* (relative to width across prezygapophyses) fall within the ranges of those of the extant Australian boids, including *Liasis* (Table 3), six vertebrae from the Wellington caves of New South Wales were longer than vertebrae of *Liasis* (Lydekker 1888, p. 256).

There is a striking resemblance between *Wonambi* vertebrae and those of *Madstoa hal* (Palaeocene-Eocene of Patagonia) and *M. madagascariensis* (Cretaceous, Madagascar) (Hoffstetter 1961a, Simpson 1933), particularly in the back-sloping neural spine, broad paradiapophyses and absence of accessory processes. Hoffstetter (1961a, b) included *Madstoa* and *Gigantophis* (from the Eocene of Egypt; Andrews 1906) in a sub-family Madstoinae. The diagnostic features were: (a) accessory processes absent; (b) a pair of parzygantral foramina present and opening into deep hollows; and (c) paracotylar foramina always present, usually as two pairs. The two genera were distinguished by the form of the ventral surface of the centrum. *Gigantophis* having an undivided haemal keel, and *Mad-*

stoia having the haemal keel distinctly divided into two. All *W. naracoortensis* vertebrae conform with character (a) and differ from other boids, all of which have accessory processes (Hoffstetter 1961a); and the more posterior vertebrae conform with (b). However all the vertebrae have distinct parazygantal foramina (even though they emerge through the characteristic deep hollow only in the posterior vertebrae) and such foramina in modern boids are minute, irregular and inconstant (Hoffstetter 1961a). *W. naracoortensis* vertebrae differ slightly from (c) in having a single pair of paracotylar foramina, but their presence at all is rare in boids (Hoffstetter & Gayrard 1964). The form of the ventral surface of *W. naracoortensis* vertebrae ranges from hypapophysis present (P16166) or haemal keel undivided (P16129t, P16144k), to haemal keel notched (P16168) and finally to haemal keel distinctly divided (P16129s and P16167); thus it encompasses the form of both *Madstoia* and *Gigantophis*. *Madstoia* differs from *Gigantophis* also in the greater development of neural spines and paradiapophyses (Simpson 1933). In these features *W. naracoortensis* closely resembles *Madstoia*.

When *Madstoia* was compared with many boids, both recent and fossil, the resemblance of *Madstoia* to *Gigantophis* was found to be closer than to other known genera. However it was impossible to conclude that the two were definitely more closely related to each other than to other fossil boids (Simpson 1933). Similarly the relationship of *Wonambi* to *Madstoia* or any other boid will remain obscure until the skull is known.

The presence of *Madstoia* in Patagonia and Madagascar has been regarded as evidence of former continuity of the southern continents (Hershkovitz 1972, p. 316).

Family ELAPIDAE

Elapid vertebrae have conspicuous accessory processes and hypapophyses on all precloacals (Fig. 1).

Pseudonaja c.f. *P. nuchalis* Günther

Material: Vertebrae (566 precloacal, 25 caudal); dentaries (6).

The vertebrae have been described (Smith 1975). The largest with a length of 11.1 mm between zygapophyses would have been derived from a snake about 190 cm long.

The dentary of *P. nuchalis* is almost straight posteriorly, but anteriorly it curves outwards then inflects sharply. The teeth are strong and

curve backwards very slightly. They are separated by a distance equal to c. 2/3 of the adjacent teeth. The second tooth is the longest but the succeeding teeth along the dentary decrease in size only slightly. The fossil dentaries are similar.

Notechis c.f. *N. scutatus* (Peters)

Material: Vertebrae—precloacal (13, length 6.3–9.9 mm, mean 7.6 ± 0.35).

These vertebrae differ from *P. nuchalis* and resemble *N. scutatus* in having a relatively short neural spine overhanging both anteriorly and posteriorly (Smith 1975).

Pseudechis c.f. *P. porphyriacus* (Shaw)

Material: Vertebrae—precloacal (55, length 4.1–9.5 mm, mean 6.3 ± 0.13); maxillae (2); dentary (1).

Both *Notechis* and *Pseudechis* have 3–5 small teeth, whereas *Pseudonaja* has 8–10 (Worrell 1963; pers. observ.). A left maxilla (P16164a) bears a curved fang, followed after a diastema, by three small, curved teeth and is consistent with *P. porphyriacus* in size and shape. A smaller fragment of a right maxilla (P16164b) is probably from the same skull, having been taken from the same sample.

P. porphyriacus dentaries differ from *P. nuchalis* and *N. scutatus* dentaries in being more sharply curved anteriorly; the teeth are fine, backwards-curving and closely-set. A right dentary (P16132e) conforms with *P. porphyriacus*.

The vertebrae have the long, acute, accessory processes (Smith 1975) typical of *P. porphyriacus* but they differ in having these processes directed more anterolaterally than in the *P. porphyriacus* available for comparison.

Undetermined

An unidentified elapid group contains 40 vertebrae (length 3.8–7.8 mm, mean 6.0 ± 1.5) characterized by the short, blunt hypapophysis.

Family VARANIDAE

Varanid vertebrae are distinguished by the overhanging condyle (Fig. 1).

Varanus varius (Shaw)

Material: Vertebrae—cervical (4, lengths 18.7–26.3 mm, mean 21.35 ± 1.76), dorsal (17, lengths—Table 4), sacral (3), caudal (26, lengths 7.9–19.2 mm, mean 12.3 ± 5.3); maxilla (1); dentaries (5); parietal (1).

The dorsal vertebrae of *Varanus giganteus* are readily distinguished by their broad centra

[ratio of width across prezygapophyses (Pr-Pr) to minimum width of centrum (BW) ≤ 1.6 (Table 4)] and long neural spines, vertical both anteriorly and posteriorly. But the vertebrae of *V. varius* and *V. gouldii* are similar morphologically—there is overlap in the relative width of centrum, relative width of condyle (CW) and relative width across prezygapophyses (all relative to the length, Pr-Po) and also in the ratio of width across prezygapophyses to minimum centrum width (Table 4). These values overlap even when the comparison is made between vertebrae from the same position in the column. The neural canal, viewed from the front, is slightly depressed in *V. gouldii* but is round in *V. varius*.

The fossil dorsal vertebrae are consistent with both *V. varius* and *V. gouldii* in their proportions and have the neural canal round anteriorly, as in *V. varius*.

Like the dorsals, the cervical and caudal vertebrae of *V. varius* and *V. gouldii* are almost (or quite) indistinguishable as to species, but the first sacral vertebrae are distinctive. The transverse processes of the first sacral of *V. gouldii* (2 specimens examined) bear several low ridges—one such ridge from the anterior-most point of the lateral surface of the transverse process extends towards the condyle; a diagonal ridge passes from the prezygapophysis to the lateral postero-dorsal tip of the transverse process and a ridge from the lateral antero-ventral tip of the transverse process to the condyle makes the posterior surface of the transverse process slightly concave. In contrast, the transverse processes are smoothly-rounded and convex in *V. varius* (3 specimens examined). Similarly in the fossils (P16135r, P16169a) the transverse processes are smoothly rounded. The fossil conforms with *V. varius* and differs from *V. gouldii* also in having the neural canal round anteriorly and the transverse processes at their lateral extremities flared to below the level of the centrum (whereas in *V. gouldii* the flaring extends more dorsally).

In *Varanus varius* the parietal foramen lies in the middle third of the length of the parietal plate (Mertens 1942), whereas in *V. gouldii* and *V. giganteus* it is in the anterior third (pers. observ.).

Laterally compressed, recurved, pleurodont teeth with striated bases are characteristic of varanids (Edsall 1969). The teeth of *V. giganteus* are fine and thin, but in *V. varius* and *V. gouldii*, and in the fossils, the lateral com-

pression is less extreme, and a labial and a lingual ridge ascend each tooth. The basal fluting extends about 1/3 of the way up the tooth.

The length of the larger fossil first sacral vertebra (18.8 mm Pr-Po) indicates a total length of c. 1.6 m for the animal.

Varanus gouldii (Gray)

Material: Humerus (1).

The shaft of the humerus is smoothly rounded in *V. varius* (2 specimens) but in *V. gouldii* (3 specimens) a distinct ridge extends from the proximal termination of the supinator crest to a muscle scar (presumably for the humeroradialis muscle) near the proximal expansion. Anteroventrally, the deltopectoral crest is prominent in both *V. varius* and *V. gouldii*, but in *V. gouldii* the crest extends further proximally than in *V. varius*. The fossil humerus (P16146b) conforms with *V. gouldii* and differs from *V. varius* in having a ridge extending proximally from the supinator crest and apparently also in the proximal development of the deltopectoral crest, although most of the proximal articular facet of the fossil humerus has been lost. The fossil has a distinct tubercle at the proximal termination of the supinator crest. Such a distinct tubercle was seen only in one modern specimen of *Varanus* species, viz. a very large *V. gouldii*. No tubercle could be distinguished in two *V. gouldii* comparable in size with the fossil, nor in two *V. varius*.

Family SCINCIDAE

In scincid vertebrae the centrum tapers, in ventral outline, from broader anteriorly to narrower posteriorly, and there is no precondylar constriction. The ventral surface of the centrum is smoothly rounded (Fig. 1).

Trachydosaurus rugosus (Gray)

Material: Osteoderms (several hundred); vertebra—cervical (10, lengths 5.2–7.0 mm, mean 6.0 ± 0.21), dorsal (46, lengths 6.1–10.7 mm, mean 8.9 ± 0.17), sacral (5 pairs), pygal (6, lengths 6.7–10.0 mm, mean 8.0 ± 0.53), caudal (5, lengths 5.0–7.0 mm, mean 6.3 ± 0.37); maxillae (5); premaxillae (2); dentaries (6); humeri (3); femur (1); frontals (2).

Osteoderms: In *Trachydosaurus*, the osteoderms are thick and coarsely pitted, whereas in *Tiliqua nigrolutea*, *T. occipitalis* and *T. scincoides* the osteoderms are thinner and finely pitted; in *Egernia cunninghami* the dorsal osteoderms bear a posterior median tooth; and in

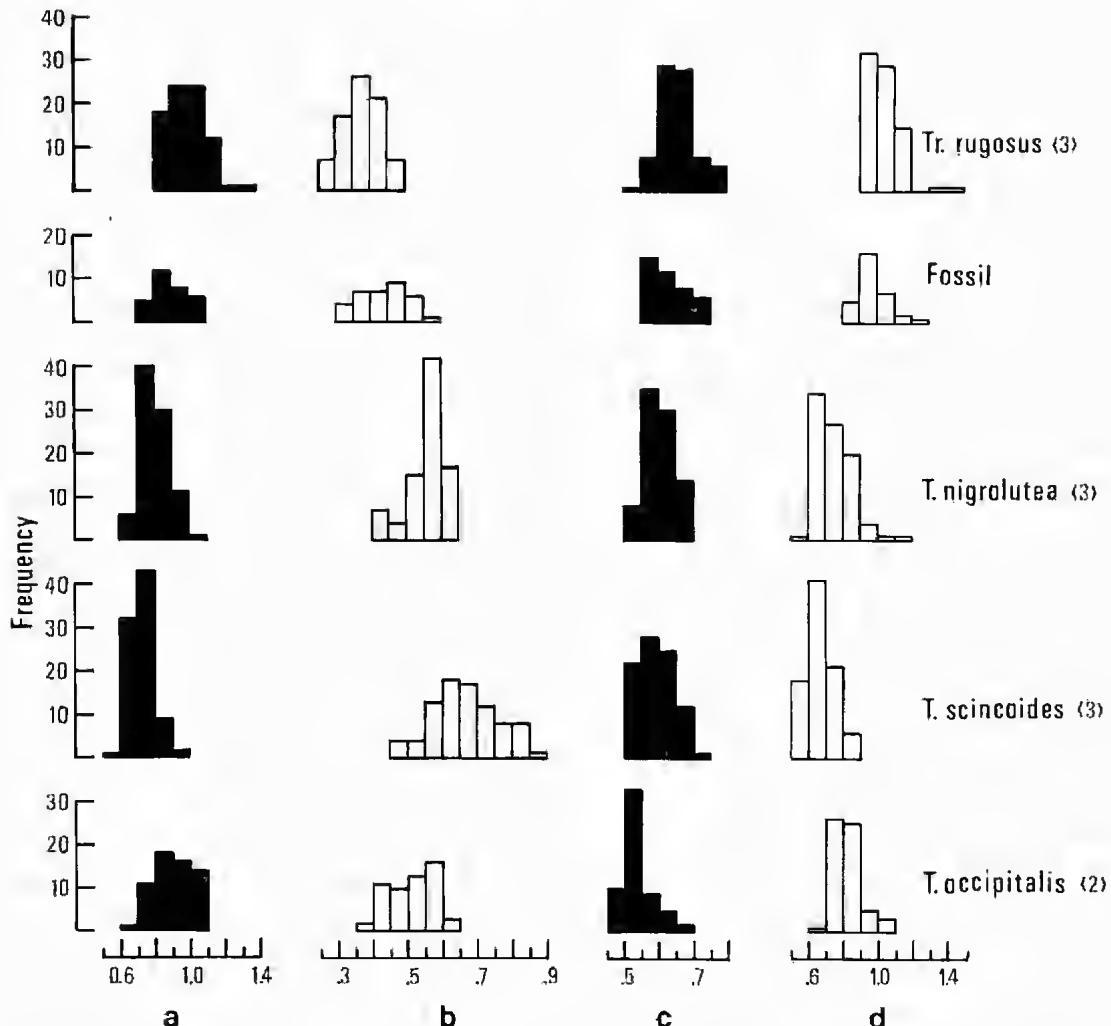


Fig. 4. Frequency distributions of some dimensions of dorsal vertebrae in which *Trachydosaurus rugosus* differs from *Tiliqua* species. The sample of fossil vertebrae assigned to *T. rugosus* has frequency distributions similar to the modern sample. (a) width across prezygapophyses divided by length between zygapophyses, (b) width across prezygapophyses divided by maximum width across paradiapophyses, (c) width of condyle divided by width across postzygapophyses, (d) height of condyle divided by width of condyle. Although the number of presacral vertebrae without a hypapophysis is 30–32, not all vertebrae could be measured in every specimen.

most other skinks the osteoderms are thin and almost smooth, except over the head of some.

Cervical vertebrae: Cervical vertebrae of scincids have the hypapophysis sutured or fused to the posterior part of the centrum whereas in agamid cervical vertebrae the hypapophyses are sutured or fused to the anterior part of the centrum (Hoffstetter & Gasc 1969). Cervicals of *Trachydosaurus rugosus* have broad, roundish zygapophysial facets whereas in *Tiliqua* species and *Egernia* species the zygapo-

physes are usually anteroposteriorly elongated and narrow.

Dorsal vertebrae: Cervical vertebrae are defined as those anterior to the first vertebra of which the rib joins the sternum (Hoffstetter & Gasc 1969), but because this distinction cannot be applied to isolated vertebrae, I have included in the discussion of dorsal vertebrae all the presacral vertebrae that do not bear a hypapophysis. Dorsal vertebrae of *T. rugosus* are squarish in dorsal outline, i.e. the width

across the zygapophyses approximately equals the length between the zygapophyses, whereas dorsals of *Tiliqua* species are longer than wide (Fig. 4a). In other skinks also, and even in the largest Australian skink, the heavily-built *Egernia bungana* (only one specimen examined), the vertebrae are longer than wide. In *T. rugosus* vertebrae, the neural spine is low, slopes backwards and overhangs posteriorly. At its posterior termination, the neural spine is thickened and marked by a short median groove. The pre-zygapophysial facets are directed dorsally at an angle to the horizontal of about 20–40° (although in the anterior 3 or 4 dorsals the angle may be as great as 60° in some specimens (Fig. 5)). The pre-zygapophysial facets extend laterally nearly as far as, or further than, the paradiapophysial convexities (Fig. 4b). The zygapophysial facets are almost round in contrast with the outwardly directed zygapophyses of agamids. The condyle is narrow (Fig. 4c) and slightly depressed (Fig. 4d). Except for the neural spine and slight zygapophysial ridges, the centrum is smoothly rounded, again in sharp contrast with agamids where not only are the lateral ridges strong, but also a wide midventral ridge is conspicuous (Fig. 4d). The ventral surface of the centrum is triangular in *T. rugosus* (as in agamids) whereas in other skinks, ventrally the sides of the centrum are almost parallel behind the paradiapophyses.

Sacral vertebrae: The pleurapophyses of the sacral vertebrae are fused distally for about one third of their length. The facet for articulation with the ilium is cupped and differs from the triangular facets of *Tiliqua* species (except *T. occipitalis*) and *Egernia* species (Fig. 6). In *T. occipitalis* where the lateral articulation is cupped (as in *T. rugosus*), the zygapophysial facets are sharply upturned, at an angle of about 40–50°, as in other *Tiliqua* species, whereas in *T. rugosus* the facets are only slightly upturned (angle c. 20°). The condyle is narrower in *T. rugosus* than in *Tiliqua* species.

Caudal vertebrae: *T. rugosus* caudals are robust and the transverse processes project only slightly ventrally, much less ventrally than in *T. scincoides*, *T. occipitalis* and *T. nigrolutea*.

Teeth and tooth-bearing bones: The teeth of *Trachydosaurus* resemble those of *Tiliqua* species in having conical tips, whereas teeth of *Egernia* species are laterally compressed at the tips (Mitchell 1950). Usually the teeth of *T. rugosus* are broad and blunt, but in some specimens the teeth are longer, thinner and

sharper. These latter overlap in form with those of the larger *Tiliqua* species. In *T. gerrardii* one tooth in each jaw is very large, about four times the thickness of the others, which are fine, with rounded tips. The maxillary bone of *T. rugosus* is robust. Beneath the orbit, a strong bone ridge runs parallel to the jaw margin and extends posteriorly beyond the level of the end of the tooth row. In *Tiliqua* species, this ridge is weaker and shorter, not extending beyond the end of the tooth row, and often ending still more anteriorly. The dentaries, too, are robust, and are thicker and deeper, especially anteriorly, near the symphysis, than are those of *Tiliqua* species.

Frontals: Two frontal bones were each characterized as of *T. rugosus* by the thick, coarsely-pitted osteoderm fused with the bone.

Limb bones: Humerus and femur have relatively thick shafts in *T. rugosus*.

Tiliqua nigrolutea (Quoy & Gaimard)

Material: Vertebrae—dorsal (6, lengths 6.0–8.9 mm, mean 7.8 ± 0.44), pygal (2, lengths 5.0, 6.2 mm), caudal (3, lengths 5.6, 6.4, 6.8 mm); maxillae (4); dentaries (3); parietal bone (1).

The size of the fossil dorsal vertebrae indicates that they were derived from a lizard at least 22 cm in snout-vent length. Such size is reached by the larger species of *Egernia* and *Tiliqua*, but not by *T. casuarinae*, *T. branchiale*, *T. petersi* nor *T. wood-jonesi*.

In *Tiliqua* species, the prezygapophyses are dorsally upturned at an angle of 35–55° (Fig. 5a) or even greater in the first two or three dorsals. The dorsal vertebrae of Australian skinks, other than *Trachydosaurus*, are longer than wide, except sometimes the last presacral which may be slightly wider than long (Fig. 4a). In *T. scincoides*, most of the dorsal vertebrae (except for the first two or three and last two or three) are extremely elongated (Fig. 4a) and this species is further characterized by the broad, depressed condyle (Fig. 4c, d) and narrow zygapophyses directed almost antero-posteriorly. In *T. scincoides*, the paradiapophyses extend laterally well beyond the lateral edges of the zygapophyses (Fig. 4b). In *T. nigrolutea* and *T. occipitalis* the zygapophysial facets are slightly wider (though the width never equals nor exceeds the length) and are directed antero- or postero-laterally; hence the width across the zygapophyses is greater (relative to, e.g., the length between zygapo-

TABLE 2

Vertebral proportions of Wonambi naracoortensis compared with those of four extant booids. Ten vertebrae were measured from the post-hypophysial region of modern specimens. The range is followed by mean \pm standard error in parenthesis.

Specimen	Length (mm)	Total height/length	Width across paradiapophyses/Width across pre-zygapophyses	Width condyle/Length	Zygosphenic width/Length
<i>W. naracoortensis</i>					
P16168	16.5	1.95	1.11	0.65	0.55
P16144k	19.4	1.99	1.09	0.65	0.65
P16144s	21.8	1.70	1.24	0.56	0.50
P16129t	16.4	2.02	1.07	0.63	0.57
P16167	23.4	1.76	7.23	0.54	0.53
P16170b	19.6	1.85	1.12	0.63	0.58
<i>Liasis childreni</i>	4.3-5.2 (4.9 \pm .09)	1.01-1.33 (1.17 \pm .03)	0.99-0.91 (0.85 \pm .01)	0.36-0.52 (0.47 \pm .03)	0.59-0.74 (0.66 \pm .02)
<i>Python spilatus</i>					
23	7.5-8.5 (8.1 \pm .09)	1.01-1.29 (1.17 \pm .03)	0.70-0.77 (0.72 \pm .01)	0.47-0.55 (0.50 \pm .01)	0.57-0.72 (0.66 \pm .02)
2*	8.1-8.8 (8.4 \pm .08)	1.24-1.47 (1.36 \pm .02)	0.78-0.80 (0.79 \pm .002)	0.53-0.58 (0.56 \pm .01)	0.65-0.75 (0.71 \pm .01)
3*	11.4-12.0 (11.6 \pm .07)	1.53-1.71 (1.61 \pm .02)	0.70-0.73 (0.71 \pm .002)	0.47-0.51 (0.49 \pm .003)	0.78-0.90 (0.85 \pm .01)
<i>Python amethistinus</i>					
1*	14.5-15.5 (14.9 \pm .08)	1.32-1.45 (1.38 \pm .01)	0.75-0.78 (0.77 \pm .003)	0.47-0.51 (0.49 \pm .004)	0.68-0.72 (0.69 \pm .004)
16*	10.1-10.5 (10.3 \pm .04)	1.42-1.49 (1.45 \pm .01)	0.79-0.82 (0.80 \pm .003)	0.59-0.62 (0.60 \pm .003)	0.63-0.65 (0.64 \pm .002)
<i>Aspidites melanacephalus</i>					
3	5.7-6.5 (6.3 \pm .07)	1.37-1.54 (1.46 \pm .02)	0.79-0.83 (0.82 \pm .004)	0.55-0.62 (0.59 \pm .01)	0.70-0.77 (0.73 \pm .01)
13	5.5-6.4 (6.1 \pm .10)	1.29-1.55 (1.43 \pm .03)	0.80-0.86 (0.84 \pm .01)	0.52-0.62 (0.58 \pm .01)	0.58-0.67 (0.62 \pm .01)
<i>Chondropython viridis</i>	5.5-6.9 (6.4 \pm .14)	0.95-1.35 (1.22 \pm .04)	0.73-0.83 (0.78 \pm .01)	0.40-0.49 (0.46 \pm .01)	0.52-0.64 (0.59 \pm .01)

* Specimen incomplete: only about one quarter of the presacral vertebrae were studied.

TABLE 3

Vertebral proportions of Wonambi naracoortensis compared with those of four extant booids. Ten vertebrae were measured from the post-hypophysial region of modern specimens. The range is followed by mean \pm standard error in parenthesis.

Specimen	W. across pre-zygapophyses/Length	Min w. centrum/Length	Height condyle/Width condyle	L. pre-zygapophysis/Length
<i>W. naracoortensis</i>				
P16168	1.55	1.12	0.82	0.49
P16144k	1.57	1.17	0.81	0.46
P16144s	1.51	1.10	0.84	0.54
P16129t	1.58	1.16	0.79	0.45
P16167	1.52	1.16	0.96	0.55
P16170b	1.50	1.12	0.88	0.56
<i>Liasis childreni</i>	1.30-1.71 (1.52 \pm .04)	0.78-1.05 (0.93 \pm .03)	0.77-1.01 (0.88 \pm .02)	0.34-0.46 (0.40 \pm .01)
<i>Python spilatus</i>				
23	1.48-1.71 (1.60 \pm .02)	0.91-1.10 (1.01 \pm .02)	0.76-0.92 (0.84 \pm .01)	0.40-0.49 (0.45 \pm .01)
2*	1.53-1.71 (1.66 \pm .03)	1.01-1.18 (1.10 \pm .02)	0.75-0.96 (0.85 \pm .02)	0.46-0.54 (0.50 \pm .01)
3*	1.74-1.88 (1.81 \pm .02)	1.14-1.25 (1.20 \pm .01)	0.96-1.04 (0.99 \pm .01)	0.54-0.59 (0.56 \pm .01)
<i>Python amethistinus</i>				
1*	1.69-1.76 (1.72 \pm .01)	1.16-1.21 (1.18 \pm .005)	0.88-0.90 (0.89 \pm .004)	0.48-0.53 (0.51 \pm .005)
16*	1.59-1.65 (1.62 \pm .01)	1.10-1.14 (1.12 \pm .005)	0.76-0.83 (0.80 \pm .01)	0.41-0.45 (0.43 \pm .005)
<i>Aspidites melanacephalus</i>				
3	1.62-1.74 (1.67 \pm .01)	1.06-1.12 (1.09 \pm .01)	0.69-0.77 (0.82 \pm .02)	0.42-0.47 (0.45 \pm .005)
13	1.53-1.63 (1.58 \pm .01)	0.99-1.08 (1.03 \pm .01)	0.75-0.82 (0.78 \pm .01)	0.40-0.46 (0.42 \pm .01)
<i>Chondropython viridis</i>	1.13-1.44 (1.34 \pm .03)	0.75-0.99 (0.91 \pm .03)	0.75-0.83 (0.99 \pm .01)	0.27-0.43 (0.37 \pm .01)

* Specimen incomplete: only about one quarter of the presacral vertebrae were studied.

TABLE 4

*Length and proportions of dorsal vertebrae of specimens of three species of *Varanus*. The ultimate presacral vertebra of each specimen is excluded. The range is followed by mean \pm standard error in parenthesis.*

Specimen	Numbers of vertebrae	Pr-Pr ₀ (mm)	BW/Pr-Pr ₀	CW/Pr-Pr ₀	Pr-Pr/Pr-Pr ₀	Pr-Pr/BW
<i>V. giganteus</i>						
	20	24.5-27.1 (25.7 \pm .14)	0.54-0.64 (0.58 \pm .005)	0.55-0.63 (0.59 \pm .006)	0.88-1.01 (0.92 \pm .007)	1.51-1.64 (1.58 \pm .008)
<i>V. gouldii</i>						
Specimen 1	20	12.4-13.6 (13.2 \pm .07)	0.48-0.60 (0.52 \pm .005)	0.52-0.56 (0.54 \pm .002)	0.86-1.00 (0.90 \pm .007)	1.68-1.78 (1.73 \pm .006)
Specimen 2	20	17.5-19.6 (18.5 \pm .09)	0.47-0.59 (0.53 \pm .007)	0.48-0.54 (0.52 \pm .004)	0.85-1.02 (0.97 \pm .009)	1.70-1.88 (1.77 \pm .011)
Specimen 3	20	14.7-15.8 (15.4 \pm .07)	0.43-0.54 (0.49 \pm .006)	0.44-0.53 (0.49 \pm .006)	0.82-0.95 (0.91 \pm .007)	1.70-1.97 (1.85 \pm .013)
<i>V. varius</i>						
Specimen 1	19	16.7-18.5 (17.9 \pm .09)	0.48-0.59 (0.51 \pm .005)	0.56-0.59 (0.58 \pm .002)	0.87-0.92 (0.90 \pm .004)	1.61-1.85 (1.76 \pm .012)
Specimen 2	16	13.9-15.4 (15.0 \pm .10)	0.45-0.57 (0.51 \pm .007)	0.53-0.57 (0.55 \pm .004)	0.84-0.96 (0.91 \pm .009)	1.70-1.88 (1.78 \pm .011)
Specimen 3	19	21.2-23.7 (22.9 \pm .17)	0.47-0.64 (0.51 \pm .009)	0.47-0.51 (0.49 \pm .002)	0.82-1.08 (0.89 \pm .011)	1.57-1.84 (1.73 \pm .015)
<i>V. varius</i> (fossil)	13	13.1-21.8 (16.3 \pm .07)	0.47-0.55 (0.51 \pm .007)	0.48-0.57 (0.52 \pm .007)	0.84-0.98 (0.91 \pm .010)	1.69-1.87 (1.78 \pm .015)

physes or to the condyle) than in *T. scincoides*. In *Tiliqua* species and *Egernia* species the tip of the neural spine may be thickened and sometimes marked with a shallow median groove, but in *T. nigrolutea* (four specimens examined) the median groove is so deep that the spine terminates in a double tip.

Three incomplete dentaries (P16124z, P16126w, and P16128h) resemble *T. nigrolutea* dentaries in shape, and four maxillae (P16125s, P16128n, P16128w and P16157z) are consistent with *T. nigrolutea* (and also with *T. scincoides* and *T. occipitalis*) in the slight suborbital ridge. A parietal bone (P16127d) is probably also of this species although the sides are slightly less constricted than in modern *T. nigrolutea*.

c.f. Sphenomorphus tympanum (Lönnberg & Andersson)

Material: Two fused sacral vertebrae.

In *Sphenomorphus tympanum*, the transverse processes of the first sacral vertebrae (S1) are strong and slant backwards only a few degrees. The transverse processes of S2 are thinner and are directed forwards to join and fuse with those of S1 at their lateral expansions. The sacral fossae between the transverse processes are wide. *S. tympanum* sacral vertebrae differ from those of *Egernia striolata* in having relatively wide fossae, and differ from *E. whitei tenebrosa* where the transverse processes of S1 are angled backwards and the transverse processes of S2 are perpendicular to the long axis of the vertebra. The fossil (P16146r) has a total length (from prezygapophysis of S1 to postzygapophysis of S2) of 3.7 mm.

Egernia, c.f. E. whitei (Lacepede)

Material: Vertebrae—dorsal (2, lengths 3.4, 2.7 mm), caudal (1, length 2.4 mm); maxillae (5 left, 5 right); dentaries (8 left, 6 right); frontals (1).

The Meckelian groove in the lower jaw is closed anterior to the splenial in *Egernia* but it is open forward to the symphysis in *Sphenomorphus*. The dentary of *E. whitei* is deeper than the slender dentary of *S. tympanum*, and the notch in the posterior lateral surface of the dentary is higher (i.e. nearer the tooth row) than in *S. tympanum*. The fossils are consistent in shape and size with *E. whitei*.

The fused frontal bones of *E. whitei* differ from those of *S. tympanum* in their gradual taper, both anteriorly and posteriorly.

Family AGAMIDAE

Agamid vertebrae are characterized by their triangular ventral outline and strong subcentral ridges.

Amphibolurus c.f. A. barbatus

Material: Maxillae (1); dentaries (7).

Agamids are the only Australian reptiles with acrodont tooth implantation. The largest fossil, a right dentary (P16132b) with length of tooth row 14.5 mm, closely resembles *A. barbatus*. The other specimens, two of them fragments, may be of a smaller species.

Faunal change

The two reptiles most common in the Victoria Cave deposit, viz. *Pseudonaja* c.f. *P. nuchalis* and *T. rugosus* were represented at all depths in similar abundance. The less common species, except for *W. naracoortensis* were also found at various depths from the surface to the present maximum depth of excavation. Seven vertebrae and the tooth fragment of *W. naracoortensis* were near the surface and all within 2 metres of each other. Hence the reptile fauna does not change remarkably with depth in the deposit.

Discussion

The small marsupial remains, together with abundant rodent remains, were probably brought into Victoria Cave by owls (Smith 1971, 1972), and the small lizards may also have been the prey of owls. Among the larger species, *Trachydosaurus rugosus* is a clumsy, short-legged, heavy-bodied lizard which might easily fall into sinkholes or caves and would have little chance of escaping. This species has been recorded from several cave deposits (e.g. Cook 1963, Finlayson 1933, Longman 1945). The snakes may have actually inhabited the cave, as live brown snakes (*Pseudonaja* sp.) are found in the limestone caves in south-eastern South Australia (Wells, pers. comm.) and *P. nuchalis* has been classified as an occasional troglobiont (Richards 1971).

In any measurements of the bones of reptiles, intraspecific variances are large because reptile growth is asymptotic. When vertebrae are the bones measured, changes along the column further increase the variation. In the identification of isolated vertebrae of some groups (e.g. the snake family Crotalidae), these inherent large variances can be offset by considering several dimensions simultaneously and in comparison with their previously determined inter-relationships along the entire column of reference skeletons (Brattstrom

1964). Nevertheless, when the reptile remains are abundant or include a qualitatively diagnostic bone (e.g. the first sacral vertebra of *Varanus*), the species can be diagnosed with confidence.

Of the 5 species confidently determined, 4 are still found in south-eastern Australia, and all but *Varanus varius* have been found near Naracoorte. All 6 additional species tentatively identified have been found near Naracoorte. The large boid is the only Pleistocene species absent now. Hence, among the reptiles, the small species have survived from Pleistocene to present without detectable change of the characters available in fossil material, whereas the large species has become extinct. Similarly with the marsupials; while many large species have become extinct [e.g. several *Sthenurus* species, *Thylacoleo* c.f. *T. carnifex* (Wells, pers. comm.), *Palorchestes* sp., (Pledge, pers. comm.)], the small species, e.g. *Bettongia* spp., *Perameles* spp., *Antechinus* spp. and *Petaurus* *brevicauda* are indistinguishable from modern species, many of which still survive near Naracoorte (Smith 1971, 1972). Among the birds, the only species now extinct, *Progura naracoortensis*, was a large bird, while all of the small species are extant. The factors that caused the extinction of so many large vertebrate species have had little perceivable effect on the small vertebrates.

The presence of *Varanus varius* together with *V. gouldii* in this Pleistocene deposit does not support the suggestion (King & King 1975) that the *indicus* karyotype (represented by *V. varius*) invaded south-eastern Australia after the separation of Kangaroo Island from the mainland, 8,000–10,000 years ago.

Most of the extant species of the Victoria Cave reptile fauna are wide-ranging with broad habitat tolerances. *Varanus gouldii* occurs in most parts of mainland Australia but is most common in sandy areas, where it lives in sand burrows (Worrell 1963). The tree-climbing species *V. varius* occurs throughout eastern Australia inside the 20° (508 mm) isohyet

(Rawlinson 1969). *Trachydosaurus rugosus* is found in inland areas of all mainland states, while *Pseudochis porphyriacus* lives in coastal to mountainous forests and swamps of eastern Australia, but does not extend into dry inland areas (Worrell 1963). The ranges of *Pseudonaja nuchalis* and the morphologically similar *P. textilis* together include most of mainland Australia (Worrell 1963), and *P. textilis* occurs also in New Guinea (McDowell 1967). None of these species extend into the cool temperate zone of the Bassian zoogeographical subregion (Rawlinson 1974). Conversely, *Tiliqua nigrolutea* is confined to the cool temperate zone, its range extending from the extreme south-east of South Australia and southern Victoria to the islands of Bass Strait and Tasmania. Naracoorte is close to the north-western limit of its range (Rawlinson 1974). *Egernia whitii*, *Sphenomorphus tympanum* and the genus *Notechis* occur in all zones of the Bassian but not in other subregions (Rawlinson 1974). Hence little palaeo-ecological information can be gleaned from them. The presence of a large proportion of the Pleistocene reptile fauna in the area at present does suggest that climatic changes during the last 30,000 years have been slight in south-eastern South Australia.

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